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DEPARTMENT BULLETIN No. 1210

Washington, D. C. ▼ May 1, 1924

SUMMARY OF LITERATURE ON BUNT, OR STINKING SMUT, OF WHEAT

By

HORACE M. WOOLMAN, Field Assistant in Cereal Disease Investigations, and HARRY B. HUMPHREY, Pathologist in Charge of Cereal Disease Investigations, Office of Cereal Investigations, Bureau of Plant Industry

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By HORACE M. WOOLMAN, *Field Assistant in Cereal Disease Investigations*, and HARRY B. HUMPHREY, *Pathologist in Charge of Cereal Disease Investigations, Office of Cereal Investigations, Bureau of Plant Industry.*[2]

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INTRODUCTION.

The world-wide importance of bunt, or stinking smut, as a factor influencing wheat production, its great antiquity as a cereal disease, and the vast amount of published matter relating to it, much of it not generally accessible, are facts seeming to justify the publication of this bulletin.

In the preparation of the subject matter it has been considered advantageous to present the data in the following historical periods:

(1) The pre-Tillet period (500 B. C. to 1755 A. D.).
(2) The Tillet-to-Kühn period (1755–1870).
(3) The Kühn or modern period (1870 to date).

The first of these periods is characterized by the almost complete absence of information based on an experimental investigation of the problem and by the preponderance of inferences and conclusions derived through hearsay and speculation. The second, or Tillet-to-Kühn period, marks the beginning of bunt investigations by the experimental method. During this period the causal relation-

[1] The manuscript for this bulletin was submitted for publication August 6, 1923.
[2] The investigations on the physiology and control of bunt, or stinking smut, of wheat, were conducted by the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture, in cooperation with the Washington Agricultural Experiment Station.

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ship between the bunt fungus and the disease was established, and the essential facts pertaining to the life history of the organism were definitely ascertained. The Kühn or modern period is characterized by a searching and detailed consideration of the more strictly pathologic aspects of the problem and an experimental study of various methods of controlling bunt. More recently, attention has been given to the study of varietal resistance to bunt and to the relation of certain growth factors to infection and the subsequent development of the disease within the host.

GENERAL HISTORICAL RETROSPECT.

THE PRE-TILLET PERIOD.

There is no doubt that bunt, or stinking smut, of wheat, due either to *Tilletia tritici* (Bjerk.) Wint.[3] or *T. laevis* Kühn, has been known to wheat growers for many centuries, probably ever since wheat became a cultivated crop. Without question it was known to Theophrastus, as well as to Vergil, Pliny, and other ancient Romans. It seems, however, that the same term was made to apply to both rust and smut by these early writers; in fact, these diseases certainly were thus confused by some writers as late as the middle of the eighteenth century. In the early English writings on the subject, mildew was used as synonymous with smut. In like manner it is found that "Mehltau" and "Brand" were used interchangeably by early German writers.

R. Bradley (*56*),[4] professor of botany in the University of Cambridge, London, 1725, says:

> We find here a fresh Scene of Mischief, from the Mildew in the first Places, which is here call'd *Robigo*, and by some *Rubigo*, is the Smut in Corn, which often spoils whole Fields, or Crops of Grain; for where this happens in any Quantity to distinguish itself, it spoils the whole Parcel of Corn for Sale, and renders it unwholesome to be used in Flower or Meal; or to be sown, we must certainly expect our Crop to produce a great deal of it. *Scaliger*, on *Theophrastus*, tells us, that Smut, or Mildew, is a certain Putrefaction, when the Dew, or Rain, that is lodg'd in the Ears of Corn, is not shaken off, but by the adventitious Heat of the Sun corrupts and putrefies. It is supposed, that this Disease happens most in enclosed Grounds, where the Air is more close than in Hills or Champain. The Remedy of this, says *Pliny*, is by sticking Laurel Branches in the Ground (that is, what we call the Bay) which will draw the blasting Vapour to them; and for this End were the Feasts, call'd *Rubigalia*, instituted by *Numa*, in the Eleventh Year of his Reign. But I differ in Opinion from Scaliger, that this Smut in Corn is the Effect of Putrefaction: My Opinion is, that all Blights proceed from Insects, for besides the Observations I have made with Microscopes, upon the Black in Corn, which plainly discovers it to be the Eggs of Insects; there is a certain Remedy found against it, by Colonel *Plummer*, late of *Hertfordshire*, which consists in steeping of Corn before it is sown, by which these pestiferous Eggs are destroy'd; so that the Corn steep'd, as he directs, will not produce any smutty Corn. The Receipt for making this Brine, for steeping of Corn, is in my Monthly Writings. [The writers were unable to obtain access to Mr. Bradley's Monthly Writings to which reference is here made.]

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[3] *Tilletia tritici* (Bjerk.) Wint. Syn. *Lycoperdon tritici* (*in* Svensk. Vetensk. Akad. Handl. 1775, p. 326, Abhdlg. d. Schwed. Akademie, Deutsch von Kastner).
Uredo caries DC., 1815, Flore franc., 5(6), p. 78.
Caeoma segetum Nees, 1816, Syst. Pilze, p. 14, pl. I, fig. 7.
Uredo sitophila Ditmar, 1813, *in* Sturm Deutschl. Flora, Abt. III, Bd. 1, p. 69, pl. 34.
Caeoma sitophilum Link, 1833, *in* Linne, Spec. Plant, ed. 6, v. 2, p. 2.
Uredo foetida Bauer, 1824, *in* Ann. Sci. Nat. Ser. 1, Bd. 2, p. 167.
Erysibe foetida Wallr., 1833, Flora Crypt Germ., v. 2, p. 213.
Tilletia caries Tul., 1847, Mem. Ustil., p. 113.

[4] The serial numbers (italic) in parentheses refer to the "Bibliography" at the end of this bulletin.

Camerarius (*73*) quotes one Merodanus as follows:

In the year 1550 the Gauls first raised wheat which they called roratum or mellitum (honeydew) referring to the odor when the head is green: but when mature there was nothing but a black, fœtid dust.

Hieronymus Bock (*47*, p. 665–666), who lived between 1498 and 1554, described bunt, but spoke of it as something already well known. Camerarius shows that the question had been raised in his day whether the causes of bunt were internal or external. He makes it clear that he regards bunt as being essentially different from the loose smuts of wheats, oats, and barley. It had occurred to him that the smuts might be fungi because they produced a black powder like the Lycoperdons. He finally abandoned this theory because he was unable to find with the microscope any such fungous threads as had been described for Mucor by Malpighi.

According to Richard Remnant (*321*), bunt had become a source of serious loss in England prior to 1637. He mentions having experimented with certain steeps as bunt preventives, but withholds any information as to their ingredients until satisfied as to their value. This is the earliest record of combating bunt by seed treatment that the writers have discovered.

The subject of smuts, in general, occupies considerable space in the agricultural and so-called scientific journals of the eighteenth century, but little of this was available to the writers, since it could not be found in the principal libraries of the United States. Enough of this early literature has been examined, however, to show the trend of thought for that period as to causes and means of prevention. It can be said that the ideas on the subject, particularly in the first half of the century, were largely empirical and charged with an admixture of superstition.

Several smuts were found listed by Dr. Caspar Bauhin (*36*), in Phytopinax, among which was *Ustilago secalina* (*Tilletia secalina*).

Three anonymous articles, probably by the same author, two of which are mentioned in Benevenuti's (*42*) notes, appeared in the Sammlung von Nature und Medicin: Breslau (1, 2, 3). A few abstracts from these articles follow:

A large amount of "*brand*" was found in the wheat in the year 1717; also some in the rye but not so much, rye being less subject to the trouble. The *brand* occurred mostly under certain conditions: (1) In low damp soil. (2) When the plants came up too slowly. (3) Where the soil had become contaminated. (4) When planted in double light, i. e., "Wenn früh oder Abends Sonn und Mond zugleich am Himmel zu sehen." (5) When new seed was planted damp. (6) In case of injurious dew.

He relates that honeydew and damp July weather had a bad influence. He quotes an unnamed writer to the effect that the sowing of damp new wheat, i. e., new wheat not fully cured, favors the production of *brand* and that it is safest to sow seed from the previous year, but that this should be held over, unthreshed, until just before sowing. The same writer informs us that many means of prevention were practiced, mostly superstitions, and cites a few, such as mixing powdered lime with the seed, sowing in the dark of the moon "in God's name," and soaking the seed in salt water for 24 hours. To prevent smut in barley, running the seed through burning straw (flaming) before sowing was sometimes practiced. He notes that smut can be produced experimentally in the window of a room as well as in the open field. He had observed

plants that produced both smutted and sound heads and that the smut heads were diseased before they emerged from the boot. He suggests that interference with sap flow may be a factor.

According to Jethro Tull (*378*), the use of salt brine for treating seed originated about 1650. A shipload of wheat had been beached near Bristol at high tide. The wheat was salvaged and, being unfit for grinding, but viable, was used for seed. This resulted in a clean crop, while fields in which home-grown seed was sown were bunted. He states, however, that this was only partially remedial, proving quite ineffectual in certain years. He seems to have had some idea that the disease was infective, as he recommends changing seed and suggests that results obtained by sowing the salvaged wheat might have been due to the fact that the wheat came from a locality where there was no smut.

Abbé Pluche (*309*) applies the term "smut" to what is unquestionably rust. This disease he attributes to the burning effect of the sun's rays which are concentrated by the small drops of dew or rain. Bunt, which he describes as a "black meal," results, he believes, from a failure of fertilization of the ovaries of the affected heads.

C. F. Meyer (*269*) believes "bunt dust" to be infective and thinks it acts by producing a fermentation of the sap. He advises treating with lime.

Aucante (*27*) maintains that treatment of the seed with lime and arsenic, as well as with corrosive sublimate, is useless and that it is injurious to germination. He believes smut to be due to atmospheric conditions. It is uncertain whether Aucante refers to loose smut or bunt, or whether he regards them as one. The article is interesting chiefly because it contains the first mention of either arsenic or corrosive sublimate as a treating medium.

J. H. Ritter (*330*), in response to Aucante's article, holds that the bunt dust is infective, but that bunt production is influenced by growth conditions under which the seed grain matures. He advises (1) sowing well-ripened and well-dried seed; (2) treating with a mixture of salt, saltpeter, lime, and wood ashes; and (3) in the long months sowing in the forenoon, in the short months in the afternoon.

THE TILLET-TO-KÜHN PERIOD.

In 1755, Abbé Tillet (*370*) proved by experiment the infective character of the bunt dust, thus establishing the first real step toward the discovery of the true cause of bunt. Tillet sowed seed artificially blackened with bunt spores alongside of rows sown to clean seed and obtained very much bunt in the former and perfectly sound wheat in the latter. He repeated his experiments at Versailles in 1759 and obtained the same results. The writers have been unable to find a copy of Tillet's original paper in the United States; consequently, they have been compelled to rely on such commentaries as are available. Comments pro and con regarding his conclusions furnished a large part of the literature on the subject from 1760 to 1800. Tillet's work and conclusions were imperfect in two respects: (1) He did not recognize Tilletia as a parasite or even as a fungus, notwithstanding the fact that he discovered the contents of bunt balls to be of uniform size and shape. (2) He regarded bunt and loose smut as differing only in degree, or merely as different stages of develop-

ment. However, he rejected the theory that rusts were related to the smuts.

Schreber (*339*) undertook to refute Tillet's conclusions in toto. He denied that bunt was infectious, basing his conclusion on the fact that a clean crop could sometimes be produced from smutty seed. He argued that bunt was due to a disordered sap produced by atmospheric conditions. He agreed with Tillet that rust was in no way related to the smuts. Even at this date there were persons who held the opposite view.

In 1763 Benevenuti (*42*) asserted that smut or bunt was an advanced stage of rust, or at least resulted from it, and that rust was caused by concentration of the sun's rays on drops of dew or rain water.

In marked contrast to Schreber's article is one by J. L. Sturler (*359*), who strongly supported Tillet. After presenting evidence of the infective nature of the disease he proceeds to a somewhat vigorous expression of his opinion of such farmers as refuse to treat their seed. Referring to the evidence he had presented, he says:

> In spite of this clear demonstration few farmers make use of this easy and cheap means of help. Deplorable blindness and unaccountable laziness! Were they ignorant and prejudicial peasants my surprise would be less. But shall not one grieve that people of another sort, some of whom belong to the first rank, should persist in their old humdrum ways and stiffneckness? I know such without having made a single experiment maintain that smut is an accidental disease of the grain which man can not anticipate or prevent and that the powder can not infect sound grain. Can an error be more plain? However, we will hope that time and the light which the society [Economic Society of Bern] is distributing will help even such impaired understandings!

Schulthess (*342*) makes what is probably the first mention of the use of copper sulphate as a treatment medium.

Tscharner (*371*) supports Tillet, but thinks bunt can be avoided by sowing old seed. Tscharner states that red spelt is less liable to bunt than white spelt, a fact observed by him in fields containing both varieties. So far as the writers can determine, this is the first mention of varietal difference in resistance to bunt.

In 1774 Johann Christian Fabricius (*105*) published a paper on phytopathology, in which he took the ground that fungi found in plant lesions were distinct organisms and not morbid plant tissues. How much influence this had on the final discovery of parasitism in its relation to plant diseases in general and smuts in particular is hard to say.

In 1783 and 1786 Tessier (*368, 369*) repeated Tillet's experiments, confirmed his conclusions, and performed some further experiments of his own. He says:

> According to the experiments of Mr. Tillet and myself, the stinking smut spreads itself by contact with great facility and multiplies rapidly.

From his own experiments he came to the conclusion that the original cause is not to be found in the proximity of bushes, kind of fertilizer used, or the nature of the soil, but thinks the disease must originate from some inherent peculiarity of individual plants. He observed that the presence of smut "powder" on the grain retarded germination. He gives a very accurate morphological description of the affected heads at different stages of their development, from just before their emergence from the boot until maturity, and of the microscopic appearance of the spores, from which one would conclude

that he was dealing with *Tilletia laevis*. He mentions several methods of prevention by means of seed treatment.

Volkart (*384*) quotes Prévost to the effect that sulphate of copper was also recommended by Tessier.

Bryant (*69*) states that the treatment of seed wheat with salt brine, soap lees, and lime had been practiced in England for generations prior to 1784. He believes it to be useless for prevention of bunt and injurious to the seed. He also states that the farmers knew it to be ineffectual, but that they persisted in it because it was a time-honored habit. He made a careful examination of the bunted heads and gave a correct morphological description of them, including the aborted stamens. He was convinced that atmospheric or other external factors caused the shrinking or hardening of the ligule at the base of the flag leaf, thus causing the young head to be compressed in emerging from the boot. This supposed interference with the flow of the sap he believed resulted in the abortion of the stamens and consequent failure of fertilization, in which case bunt was produced. Where the compression was more severe, both pistils and stamens were aborted, and loose smut resulted. This was an ingenious theory. Bryant clearly failed to discover the presence of bunt in the young head before it was subjected to this pressure. The ideas here expressed were common, in a more or less modified form, during the eighteenth century and, together with the idea of injurious or poisonous dew and disordered sap, dominated the pseudoscientific thought, at least down to the time of Tillet's discoveries. Meyen (*268*) was absolutely certain that smuts of cereals were not infectious diseases but were due to stagnation of the sap, caused by overfertilization or improper fertilization of the soil.

The work of Prévost (*312*) was a distinct contribution to our knowledge of the smuts. He observed the germination of the spores of Tilletia and the production of the primary and secondary sporidia. He also tried to demonstrate the entrance of the fungus into the seedling.

Tulasne (*377*) carefully followed up and confirmed Prévost's work and established the genus, naming it Tilletia in honor of Tillet. In his second memoir, 1854, he figures the germination and development of Tilletia as far as the formation of the secondary sporidia. There was now no logical ground to doubt the parasitism of this smut, although no entrance to the host plant had been demonstrated.

Berkeley (*43*) says that it has been known for many years that the principal diseases of cereal plants, such as rusts, bunt, mildew, etc., are of vegetable origin. Further, he states that, in spite of Unger's (*380*) attempt to overthrow this theory, the work of Cordu, Léveillé (*239*), and others had completely established the fact that the peculiar structures found in plant lesions were not modifications of the host tissue, but that they sprang from a distinct mycelium and were as certainly vegetable as other fungi. In the same article, Berkeley reports bunt studies carried on by him during the year 1846 for the purpose of demonstrating the parasitism of the organism as well as the method of infection and the physiologic relationship of the fungus to the host. He observed the germination of the spores and the production of sporidia, though he did not recognize the latter as belonging to Tilletia, but thought it a Fusarium attacking the bunt. Farther on he states that in one case he observed on a bunted plant a streak

of bunt upon the stem "in which the fetid smell and peculiar structure were not to be mistaken." Evidently he was ignorant of Prévost's work, for he says (*44*) that he believes himself to have been the first to observe the fusiform sporidia, although he misinterpreted them. In 1857 (*45*) he correctly figures the germination and development as far as the formation of secondary sporidia.

The controversy between those who recognized fungi as causes of plant diseases and those who regarded them merely as symptoms or effects of plant disorders raged from 1800 to 1860, and the briefest review of the writings of this period would extend this bulletin beyond reasonable limits. Of those who, by their investigations and writings, have contributed to the establishment of the parasitism theory, the following deserve special notice: De Candolle (*74, 75*, p. 1435–1438), Banks (*31*), Prévost (*312*), Rudolphi (*331*), Tulasne (*377*), Léveillé (*239*), Berkeley (*43, 44*), and De Bary (*34, 35*). The leaders of the opposition were Unger (*379, 380, 381*), Meyen (*268*), and Fries (*126*). In so far as bunt and other covered smuts were concerned, the controversy ended with the work of Kühn (*220, 223*), and Wolff (*398*), who demonstrated the entrance of the mycelium at the root node or between it and the point of the leaf sheath. The work of Maddox (*255, 256*), Hecke (*144*), and Brefeld (*61, 62*) in proving the blossom infection of the loose smuts put them in a class apart from the bunt and covered smuts and facilitated in great measure the further study of both classes.

THE KÜHN OR MODERN PERIOD.

Kühn (*220*) observed what he conceived to be the entrance of the fungus threads into the host plant through the leaf sheath and stated that it grew across, through the leaf layers, to the growing point.

The next successful experiments were those conducted by Wolff (*398*). He investigated several smuts, but principally the stem smut of rye, *Urocystis occulta* (Wallr.) Rabenh. His conclusions were that the rye-smut organism entered the host, not necessarily at the root node, but within 8 or 10 millimeters above it. Wolff observed that the mycelium, while passing through the epidermal cell, was inclosed in a cellulose sheath, and that after this passage its growth within the host became intercellular, pushing haustoria into the cells. With the smuts of wheat, oats, and barley, Wolff claimed that the mycelium was, in general, intracellular. In 1874 Kühn (*223*) announced that infection could take place at almost any point in the seedling.

After Kühn, Brefeld carried on an extensive series of inoculation experiments, using sporidia produced in pure culture (see Ward, *390*). He maintained that the fungus could enter the plant at any point where it could be brought in contact with meristematic tissue. He asserts also that he found the mycelium in all parts of the young growing plant, from the root hairs and roots upward, and that he obtained infection by passing the inoculum downward to the growing point through the rolled leaves by means of a capillary tube. In this latter case he says that many points of entrance could be discovered when the material was killed soon after the inoculation, but that the openings soon closed and became invisible with the growth of the plant. Brefeld used oats and barley and their smuts in his inoculation experiments, so his results may not be entirely applicable to Tilletia.

Jensen (*184*) suggested the possibility of blossom infection in case of the loose smut of barley. His deductions, based on certain experiments and observations, were briefly as follows:

(1) He was unable to produce infected plants by applying spores to the seed.

(2) Seed taken from a field in which loose smut had appeared produced infected plants in spite of treatment with copper sulphate, while seed from a clean field produced a clean crop.

(3) Seed treated with copper sulphate produced a smutty crop, while the same seed treated with hot water produced a clean crop. From these facts, Jensen reasoned that either an internal infection had obtained or that the spores were lodged between the grain and its adhering glumes.

Maddox (*255*) demonstrated the blossom infection of the loose smut of wheat. This was fully confirmed by Brefeld (*61*) in 1903, Hecke (*144*) in 1906, and Hori (*170*) in 1907.

After this date the history of the investigation of the bunt and loose smut of wheat becomes for the most part dissociated. Before taking leave of the subject of the loose smuts, a few words should be said about the contributions of Maddox to the discovery of blossom infection, inasmuch as he has never been accorded the complete recognition he deserves. His methods of investigation are best expressed in his own words, quoted in 1896 in the Agricultural Gazette of Tasmania:

I will now give the conclusions I have arrived at with smut [of wheat] from the results of my experiments. I have never been able to cause infection and reproduce the disease with spores on the grain or in the ground, which I can so easily do with bunt spores to reproduce bunt. The only way I have been able to infect grain and reproduce smut (which seldom ever fails) is by putting the spores on the ovary of the plant at flowering time, about the same time as the pollen grains are being shed. The grain will mature without the slightest signs of being diseased. I have hit the time so well now that I may say I never have a failure. I think this accounts for when I did fail, viz, the ovary was not forward enough for the spore to get its seed bed, or possibly sometimes the spores were not matured enough. The comparison of bunt and smut spores finding their seed bed are the very opposite. It is really wonderful to me how the smut spores do, as the ovary is well protected by the glumes or chaff, and there is no doubt that here we have a practical demonstration of the fact that infection by the loose smut of wheat occurs during the flowering period and that this is the first record of it.

McAlpine (*252*) in his "Smuts of Australia," 1910, accords due recognition to Maddox by quoting the foregoing paragraph. On the other hand, Kirk (*211*), in the Annual Reports of the New Zealand Department of Agriculture, gives the entire credit to Brefeld and Hecke, with no mention of Maddox.

Lang (*231*) published his conclusions from somewhat extensive investigations of the physiologic relationships of the smuts to their hosts and of their modes of infection. His studies were confined to *Ustilago tritici* (Pers.) Jens. and to the smuts of oats and barley, but it is of interest to note that he found them all to be intercellular parasites and that they obtained their nutriment through their high osmotic power. So far as the seedling infection in case of oats and barley is concerned, he is of the opinion that the entrance of the parasite is promoted by the degeneration of the cells of the leaf sheath, if not entirely dependent on it.

In the period following the final determination of the parasitism and the mode of infection of bunt and extending to the present time, much investigation has been carried on and a great volume of literature published. This work and publication can be grouped under

three general heads: (1) Physiologic and ecologic factors, (2) varietal resistance or immunity, and (3) seed treatment.

PHYSIOLOGIC FACTORS AFFECTING THE DEVELOPMENT OF BUNT.

HISTORY.

Throughout the pre-Tillet period, from Theophrastus down, the cause of bunt, as well as that of other smuts and the rusts, was sought almost entirely in physiologic and environmental factors, Bradley's supposed discovery that the bunt spores were insect eggs being the only notable exception. Theophrastus, and evidently Pliny, believed this smut to be due to moisture entering the young head, causing putrefaction under the action of the sun's heat. In all the literature of the early part of the eighteenth century we find the cause attributed to such things as dew, honeydew, fog, rains followed by hot sunshine, damp soil, interference with flow of sap, and failure of fertilization.

The experiments of Jethro Tull (*378*) furnished strong evidence that certain climatic and soil conditions were contributory factors. He cites the fact that a large amount of bunt appeared in certain years. He believed that excessive soil moisture was conducive to bunt production and finds strong support for this belief in the results of what seems to have been the earliest controlled physiologic experiment on record dealing with the bunt problem. He took up several seedling wheat plants from a field and transferred them to the window of his chamber, where they finished their growth in excessively wet soil, a part of their roots being at all times in water. These plants were entirely bunted, while bunt heads were very rare in the field from which he took up his experimental plants. Others observed that late sowings were more subject to bunt than crops sown earlier.

While Tillet's experiments proved bunt to be an infective disease, evidence has steadily accumulated to show that the occurrence of bunt in the crop is largely dependent on ecologic factors, not only at the time of sowing but to some extent during subsequent growth.

Ferle (*116*) says that dampness, protected locations, impermeable soil, and fresh stall manure favor bunt production. Ivanoff (*178*), working with *Tilletia laevis* in Tiflis, Transcaucasia, found an apparent relation between bunt prevalence and either altitude or moisture.

The first recorded observations on the relation of temperature to spore germination in Tilletia were those of Prévost (*312*) about 1807. He states that in water they germinated at 17° to 18° C. after 2½ to 3 days, at 14° to 15° after 3 to 4 days, at 11° to 12° after 5 to 6 days, at 7° to 8° after 9 to 10 days, and at 4° to 5° after 11 to 12 days. Hoffmann (*164*) and Schindler (*336*) investigated the thermolethal points of spores.

Tubeuf, in his comprehensive investigations of all phases of the bunt problem (*372, 374*), concludes that at a temperature of 3° to 4° C. the spores will not germinate, and that even at temperatures of 5° to 11° C. they may remain ungerminated in the soil and, consequently, a source of danger. He finds the optimum temperature for their germination to be between 16° and 18° C. He is in agreement with Appel that high temperatures promote bunt production.

Volkart (*384*) found that the optimum temperature for spore germination was between 16° and 18° C. Between 18° and 20° C. the germination began just as quickly, but was less vigorous. Above 25° C. there was no germination, but the spores remained uninjured. Volkart apparently did not undertake to fix the minimum. The figures in Table 1 are from a series of Volkart's experiments to determine the relative response of wheat and bunt spores to various temperatures.

TABLE 1.—*Data on germination of wheat and of bunt spores, at various temperatures according to Volkart.*

Temperature.	Wheat germination.	Spore germination.
5.0° to 6.1° C.	4 per cent on the 8th day. 93 per cent on the 12th day.	A few on the 12th day. Abundant on the 15th day.
12.0° to 12.9° C.	61 per cent on the 5th day. 97 per cent on the 6th day.	Moderate on the 5th day. Abundant on the 6th day.
17.8° to 21.4° C.	3 per cent on the 2d day. 99 per cent on the 6th day.	Abundant on the 5th day.
28.3° to 33.6° C.	9 per cent on the 2d day. 98 per cent on the 8th day.	None.
33.1° to 37.2° C.	15 per cent on the 3d day. 63 per cent on the 12th day.	Do.

Volkart (*384*), contrary to the view held by Tubeuf (*372*, *374*), concludes that the lower the temperature of the soil the greater the liability to infection.

Hecke (*147*) conducted careful experiments with spring sowings in 1907 and 1908, extending from March 3 to May 21, during which time he kept a continuous record of soil temperatures. He states his conclusions as follows: "In case of bunt, the view that the degree of infection is in inverse proportion to the temperature is without doubt correct." He also notes that this would indicate early fall sowing, which is generally known to be less infected than late. Hecke, however, does not believe that the temperature influence is limited to the germination period. He further states that there are three ways in which temperature may exert an influence: (1) It may affect the germination of the spores and the seed; (2) it may lengthen or shorten the duration of susceptibility to infection; and (3) it may limit or promote the ability of the fungus to reach the growing point of the host plant.

The field experiments of Munerati (*283*, *284*, *285*) furnished further support for the views of Volkart and Hecke. All his seedings showed a reduction of bunt with rising soil temperature, but in his case, however, the soil temperature can be inferred only, as he depends on the air-temperature records taken at a neighboring weather station.

Müller and Molz (*275*) also investigated this question (see table 2 for their results). Their temperature observations are open to the same source of error as those of Munerati, i. e., they are air temperatures from a weather station, the distance of which from the experimental plat is not stated.

TABLE 2.—*Data on influence of temperature on bunt production, according to Müller and Molz.*

Winter wheat.			Spring wheat.			
Date sown.	Bunt heads per 30 square meters.	Average temperature for 7 days following.	Date sown.	Bunt heads per square meter.		Average temperature for 7 days following.
				Red Schlanstedter.	Red Bordeaux.	
		°C.				°C.
October 5	8,040	3.31	March 14	465	165	5.6
October 26	2,970	8.40	April 2	12	13	9.7
November 23	174	2.13	April 17	17	1	7.34

While the results of these spring sowings are in harmony with Hecke's conclusions, the fall sowings appear somewhat paradoxical. At that time they challenged explanation, and to some extent they still remain unexplained. Müller and Molz's conclusion that lower temperatures promote bunt production is true only with limitations.

All agree that temperature at and subsequent to sowing is an important factor, but are not in entire accord as to what is the optimum temperature. Hecke is positive that lower temperatures favor infection. He is supported by the field experiments of Munerati, cited above.

All these investigations seem to have failed to establish the important fact that there is an optimum temperature for bunt infection and production above and below which the susceptibility or liability of wheat to bunt falls off. The authors of this paper believe that their investigations, while not entirely solving the question of temperature relations to bunt, have contributed to its solution.

Brefeld (*63*) demonstrated that on a suitable nutritive substratum Tilletia would grow saprophytically for an indefinite period with a great increase of secondary conidia and eventually would produce a spore closely resembling the chlamydospore. This had been fully confirmed by the writers, but his further conclusions, i. e., that the spores are favorably influenced and their germination promoted by passing through the digestive tract of animals, have not been confirmed by later investigation. Nor has it been shown that Brefeld was correct in assuming that infection was spread by wind dissemination of the conidia, or that the application of infested stall manure to the fields would establish a permanent and increasing saprophytic growth of the bunt organism.

Tubeuf (*372, 374*), after a comprehensive investigation of the bunt problem, states his conclusion in part as follows:

> One must assume that a distribution of the bunt of wheat from plat to plat by means of conidia in general does not take place, that spores passing through the digestive tract of animals are destroyed or injuriously affected, and that fresh stall manure is toxic to spores.

In fact, Tubeuf believes that normal germination of spores does not take place in nutritive solutions. His experiments seem to indicate the possibility of a crop being infected through bunt-infested manure if applied fresh and very shortly before sowing, particularly if the spores come from infested straw used for litter, but that danger

from this source would disappear in a short time after applying the manure.

Steglich (*356*) agrees that danger from spores introduced with stall manure lasts but a few days, because, as he asserts, manure acts as a stimulant to germination and thus causes the spores quickly to become innocuous in the absence of a host plant, as continuous reproduction of conidia does not take place in the soil. A microscopic examination of spores evacuated by swine showed 75 per cent loss of viability. Spores placed in a small sack and buried in a manure pile for 193 days had practically all germinated and become innocuous. When these were mixed with water and sprayed on seed wheat they apparently caused the appearance of three bunt heads in 15 square meters of field area.

Appel and Riehm (*20*) are confident that in no case do bunt spores in the soil survive the winters of northern Europe. At that time they believed that infection from spores in the soil seldom, if ever, occurs.

Honcamp, Zimmerman, and Schneider (*167*) conducted some experiments to determine: (1) The toxic effect of bunt fed to animals, (2) the effect on the spores produced by passing through the animal, and (3) the probability of wheat infection from manure-borne spores or from spores reaching the manure after its evacuation. They found that spores passing through the animal had in great part lost their viability, but that this loss was less pronounced in the case of swine than with other animals.

Appel and Riehm (*20*) conclude that infection of wheat by way of stall manure containing spores which have passed through the digestive tract of animals is so slight as to be disregarded in practice. Thus their results in general agree with those of Tubeuf, but are not in entire accord with the conclusions of Steglich. Although infection from spores mixed with the manure after evacuation does obtain, it is, nevertheless, slight in comparison with that resulting from spores adhering to the seed. Regarding the duration of bunt viability in the soil, Appel and Riehm maintain that in uninjured bunt balls the spores can lie in damp soil for some time without germination. Thus infection from such balls might result, provided they are able to withstand external influences and remain intact until broken by tillage or seeding operations. The spores resist cold, and in dry storage they lose but little viability in two years. Appel and Riehm further state that the conidia are resistant to weather influences so long as the soil contains sufficient moisture, but that they are destroyed by dryness. An infection due to such soil infestation would, therefore, be dependent on the soil-moisture factor.

The above conclusions regarding the life of the conidia in the soil would seem to support Brefeld's theory of the continuous saprophytic life subject only to moisture relations. It is the opinion of the writers that Honcamp and others are mistaken in this conclusion and that they have overlooked a most important factor, i. e., the organic flora of the soil. The studies of the writers have consistently shown that Tilletia grows readily enough in soil or on nutrient media as long as conditions are such as to prevent its being overrun with other organisms.

Concerning the possibility of a crop becoming infected by means of wind-borne bunt spores from threshing machines, there is little to be found in the literature. It was first suggested by Saunders,

Bedford, and Mackay (*332*), who recommended treating bunt-free seed with a strong solution of copper sulphate as a protection against such wind-distributed spores. The idea is next found in the same paper in which Maddox (*255*) presented his evidence of blossom infection of the loose smuts in 1896. Maddox here notes that bunt is very liable to appear in a fallow field lying to the lee of threshing operations.

Appel (*14*) relates a specific instance of such infection. A machine threshing a bunty lot of wheat was so situated that the dust was blown across a part of a field that was sown soon afterwards, and the crop was about half bunt in this part and bunt free in another part that was not exposed to the wind-blown dust.

PHYSIOLOGIC RESPONSE OF SPORES OF TILLETIA TO TEMPERATURE.

Hoffmann (*164*) investigated the thermolethal points of several of the Ustilagineæ, but did not include Tilletia in his experiments.

Schindler (*336*), on the contrary, confined his work to *Tilletia caries* Tul. He found that spores were somewhat injured by an exposure to 65° C. of dry heat for a period of two hours, but that the absolute death point for a 2-hour exposure was between 95° and 100° C.; that when placed in water for two hours at 40° C., they were somewhat injured; and that the death point lay between 45° and 50° C. He states that an exposure of −16° C. of dry cold for two hours was not injurious and that the spores were not killed by outdoor exposure in the soil from December 5 to January 16. During this period the average daily minimum temperature was −8.5° C. and the average maximum −1.3° C. According to Jensen, a 5-minute exposure to damp heat ranging from 52.5° to 60° C. is fatal to the spores of Tilletia. Kühn states that most of the spores are killed by a 5-minute bath at 52.5° C. According to Kirchner (*201*), they are all killed within five minutes at 55° and 56° C.

Tubeuf (*372*, *374*) germinated spores in water that had been subjected to a temperature of 37.5° to 38° C. for 24 hours. There was, however, a tendency to abnormality in the germination. He obtained no germination from those exposed for three days to a temperature of 39° to 40.5° C.

Volkart (*384*) found that spores of Tilletia would not germinate at and above a temperature of 30° C. but were uninjured at that temperature and germinated perfectly in four days when transferred to suitable temperatures.

CONTROL OF BUNT.

HISTORY OF SEED TREATMENT FOR THE PREVENTION OF BUNT.

Seed treatment for the prevention of bunt, by one method or another, has been practiced nearly three centuries. Before the true nature of the disease was known many of the more intelligent farmers conceived methods of seed treatment on the theory that the seed needed a stimulus to enable it to resist the disease, hence the use of fermenting animal manures. With the idea of the infective nature of smut came the use of toxins. The origin of the use of copper sulphate has been generally credited to Kühn, but he makes no claim to originality and credits it to Prévost, who in turn passes it back to Tessier. The fact is, it is of still earlier origin, for it was recommended

by Schulthess (*342*), and Taylor (*367*) of England recommended its use at the rate of half a pound per bushel of seed. So far as the writers have been able to ascertain, Kühn (*221*) was the first to investigate carefully the effect of copper sulphate on bunt spores as well as upon the seed and to recommend a definite formula consisting of immersion for 12 to 14 hours in a 0.5 per cent solution. His further experiments in 1873 (*222*) resulted in the conclusion that soaking for 12 hours was sufficient and that injury to seed was negligible. He found that when compared with seed soaked 12 hours in water, the treatment caused a slight reduction in the average number of roots but increased by about 30 per cent the sum total of root length. He does not state the time interval between the beginning of the germination experiment and measuring the roots, nor does he say how the grain was threshed.

Dreisch (*101*) conducted like investigations and came to a different conclusion regarding seed injury caused by the copper sulphate. He found that soaking in a solution as weak as 0.1 per cent for one hour resulted in root injury and inhibited germination by hardening the testa of the grain. He further found that such seed showed a decided difference in behavior when germinated in soil instead of in a moist chamber and that when sown in the ordinary way it suffered but little loss. He attributes this to lime in the soil and states that an aftertreatment with milk of lime counteracts the injury from copper sulphate. The only available abstract of Dreisch's article says nothing about the kind of seed used. It is entirely probable that the discrepancies between his results and those of Kühn are due to seed injury.

Nobbe (*287*) had compared the effect of copper-sulphate treatment on hand-threshed and machine-threshed grain and found the latter to be much more susceptible to injury. He found, however, that grain with abraded seed coats germinated more promptly than sound seed, which fact he attributes to the more rapid absorption of water. Like Dreisch, he found that the soil neutralized the injurious effect of copper sulphate on the seed. He believed this was due to chemical reaction between soil substances and the copper sulphate in which the toxic property of the copper was destroyed. He found support for this belief in the results of an experiment in which 152.02 grams of air-dry soil was wet with 150 cubic centimeters of a 2 per cent solution of copper salt. This was filtered off and followed by 12 washings. The total amount of filtrate was 2,240 cubic centimeters, and contained only 7 per cent of the copper salt originally added. Grassmann (*137*) investigated the effect of copper sulphate on machine-threshed wheat, immersing the grain in solutions varying in strength from 0.1 to 2 per cent. He found that the 0.1 per cent solution caused but little injury, but that the injury increased with the strength of the solution, resulting in total loss of viability at 2 per cent strength. He found also that seed injury increased with the lapse of time between treatment and sowing for a period of 10 days. Seed treated with a 0.5 per cent solution 16 hours and tested for viability showed increasing injury as follows: 24 hours after treatment, 34 per cent; 48 hours, 43.07 per cent; 72 hours, 47.64 per cent; 6 days after treatment, 51.33 per cent; 10 days after, 55.73 per cent.

Jensen (*184*) announced the results of experiments involving the use of hot water for the prevention of smut. Up to this time his studies were confined chiefly to oats and barley. This method, as

well as dry-heat sterilization, held an important place in subsequent investigations.

Experiments by Kellerman and Swingle in 1889 (*196*) and Kellerman in 1890 to 1896 (*191–194*) led them to conclude that of the many methods of seed treatment tested by them, the hot-water method was best for general use. Their experiments also established the practical value of potassium sulphid as a preventive of oat smut and the covered smuts of wheat and barley. The results of these experiments indicated that potassium sulphid reacted favorably on the germination of the seed and on the early growth and vigor of the plants. It was found that the promptest germination resulted from seed soaked 24 hours in a 0.5 per cent solution of potassium sulphid where this test was made immediately following treatment. The prompt germination and stimulation of seedling vigor were considered as factors favoring rapid growth and hence possible escape from infection.

Arthur in 1890 (*25*) concluded that seed wheat was practically uninjured by hot-water at 54° C. for 5 minutes. Experiments by Hickman (*151*) supported Kellerman's findings as to increased yield following treatment with hot water. Harwood and Holden (*143*) found that a 10-minute treatment at a temperature of 57.7° C. or less produced no change in germinative energy.

Kirchner (*201*) reviews the results of all experimental study of the Jensen method and gives the data resulting from his own experiments, which, while not extensive, were carried out with such careful regard for all factors and details as to give the results high value. His conclusions favor the Jensen method.

Geuther (*133*) suggested the use of formaldehyde as a sterilizing agent in combating smuts in general and supported his recommendation by experimental evidence. Bolley (*50*) gives the results of laboratory and field experiments in the treatment of seed wheat for the years 1893 to 1896, inclusive. In these experiments he used copper sulphate, mercuric chlorid, hot water, and formaldehyde. His is the first recorded use of formaldehyde in the United States as a fungicide for the prevention of bunt. As to the efficacy of a bunt preventive, he considered corrosive sublimate superior to all other fungicides, with the possible exception of formaldehyde, which at that time had received only preliminary tests.

Kittlauss (*213*) reported on extensive experiments regarding the injury to seed grain from the use of copper sulphate. His opinion was that the degree of damage was to some extent dependent on injury to the seed coat.

Falke (*106*) found that an application of 0.5 per cent copper sulphate for a period of 16 hours produced no injury when the seed coat was uninjured and notes that injury was greater to machine-threshed than to flail-threshed grain.

From 1900 to 1903 Farrer (*109, 110, 113, 114*) carried on extensive seed-treatment experiments, from which he concluded: (1) That bunty seed wheat could not be sufficiently cleaned by repeated washings in water to make its use safe. (2) The spores within unbroken bunt balls could not be killed by any treatment that the wheat could survive. (3) Copper sulphate was fairly efficient in killing the spores on the grain, and, although it was more injurious to the seed than either formaldehyde or mercuric chlorid, it furnished greater protection against reinfestation. (4) Formaldehyde was cheap,

effectual, and safe; and compared with copper sulphate was noninjurious to the seed, but afforded no protection against reinfestation.

Tubeuf (*372*, *374*) states that laboratory experiments seemed to show that spores of *Tilletia tritici* could be killed with an application of formaldehyde gas that would not injure seed wheat, but in field experiments as high as 15 per cent of smut occurred in the crop grown from seed thus treated. Damp grain was severely injured by the gas treatment. The use of gas, therefore, was not recommended.

According to Tubeuf, a 12-hour treatment with a solution of 0.5 per cent copper sulphate reduced the yield of both plants and heads. The injury caused by copper sulphate he reduced by an afterbath in milk of lime. Machine-threshed seed he found to be more susceptible to copper-sulphate injury than flail threshed. All grain treated with copper sulphate germinated better in earth or sand than in filter paper. Disinfection with hot water at 55° to 56° C. for 15 minutes resulted in complete freedom from bunt and no injury to seed, but he considered its use inconvenient. Seed which had been washed in water and subsequently immersed in a 0.1 per cent solution of formaldehyde for a period of 4 hours, followed by quick drying, showed no resultant injury. This treatment he found thoroughly effective in killing the smut spores, and he also proved Bordeaux mixture to be entirely effectual but likely to result in seed injury if the action is too prolonged.

Tubeuf (*374*) gave attention to the effect of incrusting the seed with material containing (1) nutritive substances, such as Chile saltpeter, potassium salts, kainit, and superphosphate; and (2) toxic substances.

Peacock (*295*), using copper sulphate at the rate of 1 pound to 4 gallons of water in an open tank from 5 to 10 minutes, obtained an average of 86.3 per cent germination and a bunt-free crop. A lot of seed resmutted after treating produced 4.5 per cent of bunted heads. Another lot, washed after treating and resmutted, produced 10 per cent of bunted heads, while an untreated check plat gave 35 per cent of bunt.

Falke (*108*) found that injury from formaldehyde treatment is entirely prevented by rapid drying at 51° to 53° C. Volkart (*384*) published the results of a careful and comprehensive inquiry into the effects of the various treatments upon both the spores of bunt and those of oat smut, as well as upon the seed and the resulting harvest yield. Regarding the treatments with copper sulphate, the work showed conclusively that Tilletia spores were not killed in the ordinary methods of its use, but only delayed or at best prevented from germinating, and that the viability of the spores could be restored by washing in either dilute hydrochloric or acetic acid or by placing the spores in the soil. He found for Tilletia, as Hecke had found for covered smut of barley, *Ustilago hordei*, that a reaction took place between the spores and the copper sulphate in which the copper ion united with some element of the epispore to form a compound insoluble in water, while the sulphate ion forms a soluble compound with some element or compound drawn from the spore. It follows from this that when a solution of copper sulphate is being used in farm practice for treating wheat that contains a large amount of bunt it will lose effectiveness much more rapidly than when the wheat is comparatively clean. It was found that the lethal effect of copper sulphate was increased by raising the temperature of the treating bath from

20° to 33° C. With formaldehyde, no germination was observed in spores treated 2 hours in a 0.1 per cent solution. Those treated 1 hour and washed gave complete germination in 14 days, while untreated spores gave complete germination on the fifth day.

Sutton and Pridham (*362*), Ditzell and Downing (*93*), Sutton and Downing (*361*), and Soutter (*348, 349*) performed some experimental work to determine what fungicidal treatments gave the most effectual protection against infection through reinfestation of the seed. They all agree that copper sulphate gave the most satisfactory results.

In 1918 Darnell-Smith and Ross (*94*) reported on three years' experiments in the use of dry copper carbonate as a seed treatment for bunt prevention. They found it effectual as a fungicide and noninjurious to the seed. In fact, they believed it stimulated germination and increased the yield. These conclusions have been fully confirmed in experimental results obtained by Mackie and Briggs (*254*).

Störmer (*357, 358*) studied the relative merits of a number of treating processes, in both laboratory and field, in 1909 and 1910. He asserts that a 16-hour immersion in a 0.5 per cent solution of copper sulphate kills the spores in unbroken balls. This statement is open to question and is not confirmed by results obtained by other investigators. He failed to restore viability to spores treated with copper sulphate by washing them with 0.5 per cent solution of hydrochloric acid.

Hiltner (*155*) and Hiltner and Gentner (*161*) urge the use of mercuric chlorid as a treatment for the seed of winter grains, chiefly as a protection against Fusarium and other soil fungi. Their experimental evidence of a resultant increase in plant vigor and in the prevention of winterkilling is so convincing as to warrant our consideration of its more general adoption as a bunt preventive.

Riehm (*326*) conducted some experiments on the lethal effect of certain synthetic dyes on Tilletia spores and found that none of them killed the spores in the unbroken ball. Spores in balls, treated 10 minutes in a 1 per cent solution of Antiavit green and Antiavit blue, were delayed in germination. Free spores were killed by Antiavit blue, Antiavit green, Antiavit, Victoria blue, and acid violet, but chlorophenate of mercury, 0.05 per cent solution, killed spores in one hour with negligible injury to the seed grain.

Lehn and Vasters (*237*) found that the amount of spores carried on the seed grain was approximately proportional to the percentage of bunt in the resulting crop. Gentner (*132*) found treatment with mercuric chlorid a perfect protective against Penicillium and Fusarium, while formaldehyde promoted the attack of these fungi. He says this fungicide is much used in Denmark, Sweden, and Russia in the treatment of seed wheat and rye.

Remy and Vasters (*322*) experimented with a proprietary fungicide known as Uspulun, the active principle of which is chlorophenate of mercury, which is reported to afford perfect control of bunt without injury to the seed when used in a strength of 0.25 per cent for an immersion period of one hour.

Weck (*391*) records the results of experiments with Uspulun, which he carried on for three years. He found that the action of this fungicide as a bunt preventive was perfect, that the viability of the seed was unaffected, and subsequent growth of the seedling was stimulated.

Müller and Molz (*275*, *276*) report on additional methods of seed treatment. Germination tests were made in moist chambers and in the open field involving the sowing of 8,000 grains in each trial. Entire bunt prevention was obtained in but one case, viz, when paraformaldehyde was used, but this fungicide showed the highest degree of seed injury.

Reynolds (*323*) performed extensive experiments with many fungicides to determine their protective properties against reinfestation. His conclusions were that any treatment involving the use of copper sulphate, except immersion in Bordeaux compounds, was highly protective, and that aftertreatment with lime reduced the protection. Dry copper carbonate mixed with the seed gave the best results.

Saunders, Bedford, and Mackay (*332*) in 1893 recommended copper sulphate in preference to other media for treatment because of its protective action against infection from bunt-infested soil. But so far as the authors have been able to ascertain no experiments of this kind had been undertaken in highly infested soil. It was thought that a sufficient amount of soluble toxin might be made to adhere to the seed to establish an immunizing zone around the grain which would prevent or reduce the infection from infested soil. Obviously it could not be expected that protection by means of seed-borne fungicides could be made to extend to the surface of the soil, but it was hoped that it would be effectual in the region where the seedling s most subject to infection, i. e., immediately above the seed.

VARIETAL RESISTANCE TO BUNT.

In 1764 N. E. Tscharner (*371*) stated that for several years he had sown a mixture of red and white spelt and always found much less bunt in the former. It was not until 130 years later, however, that a scientific search was begun for resistant varieties.

In 1900 William Farrer (*110*), the noted wheat breeder of New South Wales, reported on a number of varieties which he had studied. His investigations must have been made under severe conditions, for with two exceptions the average percentage of bunt was 83.

Kühn (*225*) noted that certain varieties were less susceptible to bunt than others and suggested that this fact might be related to moisture content of the plant, i. e., that low moisture content might enable the plant to resist entrance of the mycelium or to check its spread within the host.

Tubeuf (*372*, *374*) gives in great detail the results of extensive varietal resistance experiments. He noted the number and percentage of plants partly bunted, as well as the number of sound and bunted heads appearing in each of such plants. Tubeuf is of the opinion that resistance is correlated with the varietal characters of prompt germination and rapid growth up to the point where infection is inhibited, i. e., the appearance of the first leaf. He found Ohio,[5] Ontario, and Bestehorn's Ueberfluss highly resistant. He suggests the possibility of increasing the resistance of a variety by selection through a long period of years. He found no uniform improvement as a result of selection for only one year.

Appel and Gassner (*15*) mention Ohio and Strubes Grannenweizen as being constantly resistant. Kirchner (*204*) published the results

[5] So far as the writers have been able to determine, this wheat is unknown in the United States.

of studies begun in 1903. He tested 208 varieties, including both winter and spring wheats, of *Triticum vulgare*, *T. compactum*, *T. turgidum*, *T. durum*, *T. spelta*, *T. dicoccum*, *T. polonicum*, and *T. monococcum*. The results varied from 0 to 85.92 per cent bunt. Ohio was bunt free for 1905 and gave 0.7 per cent bunt in 1906. In most winter varieties that were tested in both years, 1903 and 1904, the percentage of bunt was much larger in the crop of the second year. The 1903 sowing was made on September 9 and that of 1904 on October 7. One variety of einkorn was tested for three years and in all three was bunt free. In his article published in 1908, Kirchner (*206*) expresses doubt as to resistance being dependent on quick germination and growth as a varietal character, though he concedes that such characters would lessen liability by shortening the period of susceptibility. He says it is necessary to investigate closely to what extent these traits are inherent transmissible characters rather than changeable phenomena due to external factors. Kirchner continued his investigations up to 1916. Important reports were published by him in 1913 (*207*) and 1916 (*208*). He (*209*) states that his investigations have been carried on since 1903, during which time he has tested for resistance to bunt 241 varieties of winter wheat and 119 of spring wheat. In winter wheats he found Cimbal's Fürst Hatzfeld and Hohenheimer No. 77 very resistant. The last named was attacked in his experimental plats but four times in 10 years. Some of the Galician wheats gave favorable, though somewhat inconstant, results. Beardless Odessa was tested six times, four tests being smut free, while one gave 2.5 per cent of bunt and another 0.56 per cent. These results agree with those obtained by Hecke (*144*, *146*). Miracle, a smooth, red rivet wheat, was bunt free four years in succession. Kirchner found the durum wheats generally hard to infect, and two varieties proved very resistant. He described them as white, hard, smooth, the awns of one variety black, the other white. The Polish wheats were hard to infect. Of the spelts, two blue ones never showed infection. He notes that the same botanical group will contain varieties of high and low susceptibility. He recognizes external factors as having a great influence on infection, and he agrees with Hecke that degree of resistance is a constant hereditary varietal character. He was unable to establish any relation between germinative power and resistance. His observations led him to the conclusion that resistance is dependent on chemical composition and that the acid content of resistant varieties is comparatively higher than that of susceptible ones possessing the same morphological characters. In 1909 Pye, of Australia (*315*), stated that for several years he had been trying to obtain resistant varieties possessing other desirable qualities by crossing resistant varieties with other high-typed wheats which possessed some resistance. In these crosses he made considerable use of Medeah, a bearded durum. In his varietal tests, the highest percentage of bunt obtained was 58. The well-known wheats shown in Table 3 are selected from his results.

McAlpine (*253*) reports the following percentages of bunt infection: Federation, 88 to 100; Ohio, 4.3; Genoa, 4.5.

Hecke, in his admirable paper, "Der Einfluss von Sorte und Temperatur auf den Steinbrandbefall" (*147*), in 1909, gives the results

of exact and comprehensive experiments which are of high scientific value in that he takes into consideration the temperature factor in tests of varietal resistance. Ohio wheat, previously almost immune, in his experiments yielded as high as 61.9 per cent of bunted heads.

TABLE 3.—*Comparative resistance to bunt shown by well-known varieties of wheat in Pye's experiments.*

Variety.	Percentage of bunt.	Variety.	Percentage of bunt.
Queens Jubilee	58.00	Mudgee	6.00
Federation	49.00	Cedar	14.00
Bobs	43.00	Florence	3.03
Medeah	0	Genoa	2.01

Hecke's conclusions in part are that resistance is a varietal character and is transmissible to the progeny in crosses, but that it is modified by other factors, one of which is temperature, and that varieties react differently to external factors, temperature in particular. He is very skeptical as to resistance being constantly related to the characters of prompt germination and growth, though he recognizes the fact that the shorter the time from the beginning of germination to the appearance of the first leaf, all other factors being equal, the less the liability to infection.

Darnell-Smith (*91*) finds no evidence that rapidity of growth is related to resistance, but notes that Florence, Cedar, and Medeah, all resistant, have but little brush as compared with susceptible varieties and suggests that this lack of capacity to hold a larger amount of spores may be a factor. Cobb's (*84*) observations on the amount and character of the brush of the variety Medeah confirm those of Darnell-Smith.

SUMMARY.

Bunt of wheat has been known from very early times and is referred to by Theophrastus and other early Greek and Roman writers.

Down to the time of Tillet (1755) bunt was believed to be caused by environmental or providential influences.

In 1755 Tillet proved by experiment its infective character.

Prévost (1807) demonstrated the fungous origin and nature of bunt.

Kühn (1858) established the fact that bunt arises from infection of the wheat seedling.

The use of copper sulphate as a bunt preventive was first suggested by Schulthess in 1761, and Kühn (1866) first evolved a formula for its use.

The hot-water treatment of seed grain for the prevention of smuts was recommended by Jensen in 1888.

The use of formaldehyde as a general seed disinfectant was suggested by Geuther in 1895.

Maddox (1896) demonstrated that loose smut (*Ustilago tritici*) is caused by a fungous infection of the blossom, thus establishing the fundamental difference between bunt and loose smut.

Appel (1913) recorded the observation that a bunty crop was caused by spores blown from a threshing machine.

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[Owing to the fact that many of the published contributions to our knowledge of bunt, or stinking smut, of wheat, were not accessible to the writers the bibliography here presented is not exhaustive. The originals of the references marked with an asterisk (*) were not available and were not examined. Many titles bearing on the subject appear in the bibliography which are not cited in the text.]

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